

Spawning Demographics and Juvenile Dispersal of an Adfluvial Bull Trout Population in Trestle Creek, Idaho

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Abstract.—We utilized a screw trap, trap-box weir, remote passive integrated transponder tag (PIT) detection weir, and otolith microchemistry to evaluate (2000–2004) spawning demographics and migration patterns of adfluvial bull trout *Salvelinus confluentus* in Trestle Creek, Idaho, a tributary to Lake Pend Oreille. Annual repeat spawning was more common than alternate-year spawning. Annual growth, estimated from adult bull trout PIT-tagged in 2000 and recaptured in 2001, averaged 28 mm. Peak diel movement of adult bull trout occurred after sunset. Emigration of juveniles occurred in two pulses, one in spring that was associated with snowmelt runoff and increasing water temperatures and a second in fall as stream temperatures dropped and fall rains began. Juvenile bull trout moved a mean rate of 455 m per night in 2001 and 423 m per night in 2002. Each year we trapped large numbers of age-0 bull trout that appeared to be emigrating with high spring flows. Based on otolith microchemistry, most of the 47 adults in the sample had emigrated at age 3 or age 4, and none had emigrated at age 0. This suggests that age-0 emigrants are not making a significant contribution to adult returns.

Bull trout *Salvelinus confluentus* remain widely distributed and occupy most of the subbasins representing their potential range (Rieman et al. 1997), yet their abundance and downward population trends remain a concern in some areas (Rieman and McIntyre 1993; Epifanio et al. 2003). Rieman and Myers (1997) analyzed redd-count trends for bull trout from Idaho's Lake Pend Oreille as well as Montana's Flathead Lake and Swan Lake basins and concluded that the predominant pattern was one of decline in both the Lake Pend Oreille and Flathead Lake basins. The authors further concluded that declines were not universal as demonstrated by the population growth in the Swan Lake basin. Concern over the population status and trends of bull trout was underscored by the listing of the Columbia River bull trout population segment as threatened under the Endangered Species Act in 1998. However, during the past decade, bull trout redd counts measured in the Lake Pend Oreille basin suggest improving populations in many tributaries (Downs and Jakubowski 2005).

Diverse life history strategies are important to the stability and persistence of populations, such as variation in the timing of juvenile emigration and frequency of spawning (Rieman and McIntyre 1993). However, few studies published in the literature have described the life history characteristics and demographics of adfluvial bull trout. Fraley and Shepard (1989) studied and reported on the life history of adfluvial bull trout in the Flathead River system, and Pratt (1992) summarized and synthesized the findings of numerous authors in a general overview of bull trout life history across its range. Other authors have described aspects of bull trout life history, such as migration characteristics (Swanberg 1997a, 1997b; Brenkman et al. 2001; Schmetterling 2003) or habitat use and patch size (Nakano et al. 1992; Rieman and McIntyre 1993, 1995; Saffel and Scarnecchia 1995; Thurow 1997; Bonneau and Scarnecchia 1998; Muhlfield et al. 2003; Wissmar and Craig 2004).

We present information collected using sampling techniques that have not been widely applied to bull trout or other inland salmonids. We applied passive integrated transponder (PIT) tag technology and analyzed otolith structure and chemistry to estimate bull trout spawning frequency, growth, age, and migratory patterns. Because the chemical composition of the otolith (i.e., strontium/calcium ratio) is positively

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correlated with water chemistry and remains unchanged after deposition, the otolith provides a permanent record of migration and habitat use. Previous otolith research has focused on migration between freshwater and marine environments (Radtke 1995; Limburg 2001); rarely has the technique been applied wholly within freshwater systems (Kennedy et al. 2000; Wells et al. 2003).

The data we report represent information collected as part of an ongoing research project evaluating juvenile bull trout survival rates in Lake Pend Oreille. Our research objectives were (1) to estimate spawning frequency and growth for adult bull trout, (2) to determine the age at out-migration for returning adults, and (3) determine seasonal juvenile migration patterns. Through our study, we hoped to provide a more complete picture of bull trout life history and biology that would be useful to population managers and modelers (e.g., Rieman and Allendorf 2001) and improve our understanding of bull trout population responses to habitat changes and management actions.

Study Area

Lake Pend Oreille is Idaho's largest and deepest natural lake and is located in the panhandle region of northern Idaho. The lake has a surface area of about 33,700 ha, has a maximum depth of 351 m (Rieman and Falter 1976), and is classified as oligotrophic. Both the world record bull trout (14.5 kg) and rainbow trout *Oncorhynchus mykiss* (16.8 kg) were caught in the lake in the first half of the last century. Native salmonid species include bull trout, westslope cutthroat trout *Oncorhynchus clarkii lewisii*, mountain whitefish *Prosopium williamsoni*, and pygmy whitefish *Prosopium coulterii*. Nonnative salmonids include brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, kokanee *O. nerka*, lake trout *Salvelinus namaycush*, lake whitefish *Coregonus clupeaformis* and rainbow trout.

Trestle Creek, a third-order tributary to Lake Pend Oreille, drains approximately 5,950 ha of the Cabinet Mountains in northern Idaho and supports the largest bull trout population in the lake system (Epifanio et al. 2003; Figure 1). Historically, fishery management of Lake Pend Oreille has focused on providing a harvest fishery for kokanee and trophy fisheries for rainbow trout and bull trout. The lake supports primarily adfluvial populations of bull trout distributed in multiple spawning tributaries to the lake. To protect spawning adult bull trout, all tributary streams to Lake Pend Oreille except the Clark Fork River have been closed to bull trout harvest since 1964, and Trestle Creek has been closed to fishing since 1988. Bull trout redd counts in Trestle Creek have averaged 258

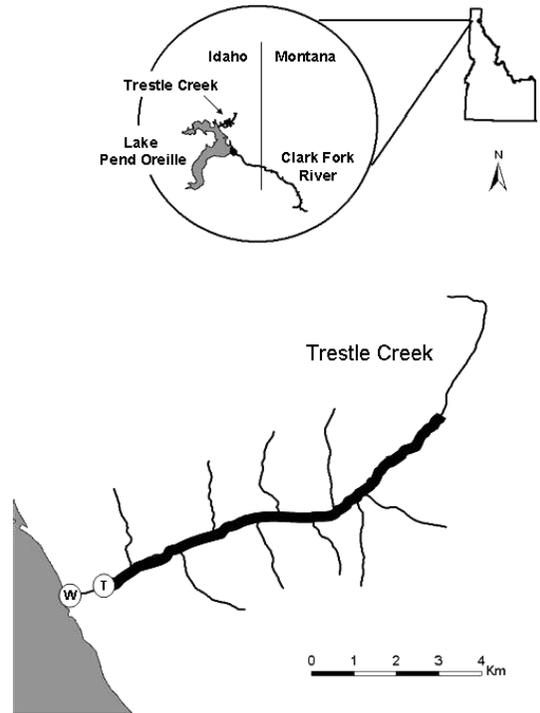


FIGURE 1.—Location of passive integrated transponder tag weir (W) and bull trout traps (T) on Trestle Creek, a tributary to Lake Pend Oreille, Idaho. The thickened portion upstream of the trap delineates the primary adfluvial bull trout spawning area.

annually since counts began in 1983 (Downs and Jakubowski 2005), and mark-recapture population estimates indicated a total 1998 spawning escapement of 1,387 adults (Dunham et al. 2001). Adult bull trout enter into Trestle Creek as early as May, and upstream migration continues into October (Downs et al. 2003). Peak spawning occurs in September.

Methods

Adult spawning frequency and growth.—We used a 1.52-m rotary screw trap (Kennen et al. 1994) to capture, mark, and recapture adult (>275-mm) and juvenile (≤ 275 -mm) bull trout migrating within Trestle Creek from 2000 through 2002 (Figure 1). Trapping was conducted from April 4 to November 4 in 2000, from March 29 to November 24 in 2001, and from March 12 to December 13 in 2002. The screw trap was operated intermittently during the fall (from mid-September through mid-November), because of peak leaf-fall and the capture of large numbers of emigrating adults. During those 2 months, trap operations averaged 2 nights/week in 2001 and 4 nights/week in 2002. In 2000, we also used a picket-style weir with

a trap box (Nelson et al. 2002) during late summer and fall months when flows were too low to operate the screw trap. Although the weir had an upstream and downstream trap box, its function was primarily to capture emigrating fish.

Captured bull trout were anesthetized, examined for marks, scanned for the presence of a PIT tag, and measured (total length [TL]; mm). In 2000 and 2002, if an adult bull trout was not previously tagged, a full-duplex PIT tag (11.5×2.1 mm, 134.2 kHz) was inserted into the soft tissue of the cheek, parallel with the dorsoventral plane of the fish. Adult bull trout were not PIT-tagged in 2001. Fish were held for several minutes in freshwater and then released back into calm water near cover.

In 2001, we installed a remote PIT tag detection weir approximately 1.4 km downstream of the screw trap and weir site, at the mouth of Trestle Creek. The structure consisted of a picket weir and modified trap box that was designed to detect PIT-tagged fish moving in and out of Trestle Creek. Pickets were spaced 25.4 mm apart to allow the movement of juvenile fish through the weir panel. The weir panel guided fish through a cone-shaped entrance into a metal frame trap box that was covered with 6.35 mm black plastic mesh netting. The cone tapered to an opening 175 mm in diameter that was surrounded by a waterproof PIT tag reading antennae. As PIT-tagged fish passed through the antennae the frequencies were recorded on an FS-2001 PIT tag reader (Destron-Fearing Corporation) that was enclosed in an ammunition can mounted on top of the trap box. Time of movement was determined by comparing the time stamp for each record on the PIT tag reader with the sunrise and sunset times for Sandpoint, Idaho (www.sunrisesunset.com).

The remote PIT tag weir was operated intermittently from June 29 to July 27 and then continuously from August 28 to November 14, 2001. The PIT tag weir operated continuously from August 30 to October 31, 2002, and almost continuously from July 17 to October 24 in 2003. In 2004, the PIT tag weir operated almost continuously from June 22 to October 15. These dates were the most effective for sampling emigrating postspawn adults; a large proportion of the upstream migrating adults probably entered Trestle Creek before installation of the PIT tag weir in some years. All of the traps, as well as the PIT tag detection weir, were located in the lower reaches of Trestle Creek, downstream of the primary bull trout spawning and rearing area (Figure 1).

Captures in the screw trap and detections at the remote PIT tag weir enabled us to estimate the frequency of repeat spawning by comparing the

number of adult bull trout marked in 2000 or 2002 with the number of those fish detected in subsequent years. Individuals detected in two or more successive years in Trestle Creek were labeled "annual" spawners, and those that were detected in alternating years were labeled "alternate year" spawners. Growth of adult bull trout was estimated as the difference in length between capture in 2000 and recapture in subsequent years.

Age at emigration for returning adults.—In fall 1998 and 2000 we walked Trestle Creek to search for bull trout carcasses in and near the stream channel as part of an unrelated study. All carcasses were found within the spawning reach (Figure 1). We removed sagittal otoliths from each fish for use in our analysis of age at emigration. Otoliths were stored dry in polyethylene vials and were prepared in the laboratory following the methods in Zimmerman and Reeves (2000). We took digital images of each otolith through a compound microscope, and two independent readers analyzed the annual growth increments to determine the age of the fish.

The chemical composition of the otolith was analyzed with a Cameca SX-50 wavelength dispersive microprobe. We used a 15-kV, 50-nA, 5- μ m-diameter electron beam for all of our analysis. We sampled two independent transects that extended from the primordium to the outer edge of the otolith; points were spaced 35 μ m apart. We determined the point (i.e., age) when bull trout emigrated to Lake Pend Oreille, for the first time, by the marked drop in the Sr/Ca ratio along the transect (Figure 2). The season of first emigration was identified by locating the point of movement on the otolith, relative to the annuli. We assumed that the fish emigrated during spring if the point at which Sr/Ca

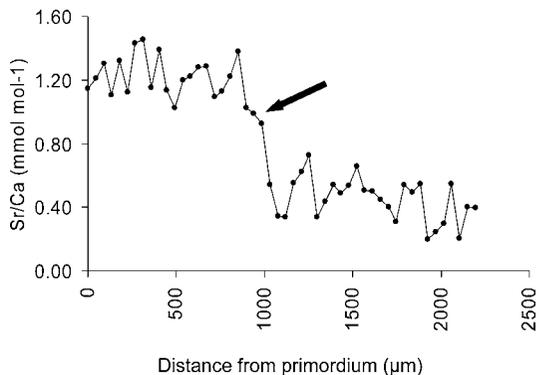


FIGURE 2.—Otolith microchemistry data for an adult bull trout from Trestle Creek, Idaho. Each point represents a sample on the surface of the otolith that was measured along a transect extending from the primordium to the outer edge. The arrow indicates where the fish left the stream environment and moved into the lake environment.

declined was on or immediately after an annulus. If the drop occurred between annuli, the fish moved in summer, and if the drop was immediately before an annulus the fish moved in fall.

Seasonal timing and rate of juvenile migration.—Juvenile bull trout were captured in Trestle Creek using a rotary screw trap, as described for adults. Similar data collection methods were employed for both adults and juveniles. However, if a juvenile bull trout was not previously tagged, a PIT tag was inserted into the abdomen of individuals greater than 75 mm. Total catch for each day was plotted against date to describe seasonal movement patterns. We estimated a downstream migration rate of juvenile bull trout within Trestle Creek by dividing the distance moved between the upstream trapping release sites and the downstream remote PIT tag station by the number of nights of travel.

Relative stream discharge was measured by a staff gauge. Water temperature was recorded by a hand-held thermometer at the time of trap check, which typically occurred in the morning. We summarized our catch data for both age-0 and age-1 and older emigrants by three gauge-height levels (≤ 25 cm, >25 to ≤ 50 cm, and >50 cm) and four temperature intervals ($\leq 3^\circ\text{C}$, $3.1\text{--}6.0^\circ\text{C}$, $6.1\text{--}9.0^\circ\text{C}$, and $>9^\circ\text{C}$) across all years. Under the null hypothesis, the number of days on which zero fish were caught for each age-group would be distributed in proportion to the distribution of all sampled days across the 12 possible temperature and gauge-height combinations. We used the chi-square goodness-of-fit test to test the null hypothesis. We further explored the relationship between gauge height, temperature, and trap catch by performing two single-factor analysis of variance (ANOVA) analyses on $\log_e(x+1)$ transformed catch data to test the hypothesis that mean catch per day was the same across the gauge height and water temperature bins for each age-group.

Results

Adult Spawning Frequency and Growth

In 2000, we captured 89 adult bull trout with the screw trap and 753 with the weir as they moved downstream postspawn, primarily in September and October, and we marked 429 of them with PIT tags. In 2001, 237 of the 429 adults tagged in 2000, were detected at the remote PIT tag weir or screw trap (Table 1). Eighteen bull trout tagged in 2000 and not detected in Trestle Creek in 2001 were detected in 2002. An additional six adult bull trout tagged in 2000 were detected in Trestle Creek in either 2003 or 2004 but not in 2001 or 2002. Seventeen individuals were detected in Trestle Creek in all 5 years of the study.

Eighteen adults that were marked with PIT tags in

TABLE 1.—Returns to Trestle Creek of adult bull trout originally tagged with passive integrated transponder tags in Trestle Creek, Idaho, in 2000 ($N = 429$) and 2002 ($N = 245$). New returns refer to bull trout that were tagged but not detected in a previous return year.

Return year	2000 tagged fish		2002 tagged fish	
	Total returns	New returns	Total returns	New returns
2001	237	237		
2002	161	18		
2003	89	4	76	76
2004	30	2	28	16

2000 and skipped spawning or were not detected by the PIT tag receiving station in 2001 returned to spawn in 2002 (Table 1). Of all 429 marked fish that spawned in 2000, 255 returned to spawn in either or both of 2001 and 2002. Annual repeat spawners comprised 93% of the total individual returns detected, whereas 7% appeared to spawn in alternate years.

In 2002 we marked 245 adult bull trout with PIT tags and 76 of those fish returned to spawn in 2003. Only 16 individuals appeared to skip a year (2003) and returned to spawn in 2004 (Table 1). We estimated that 83% of the marked group returned annually.

We recorded 280 detections from 166 individual adult bull trout in 2003 and 103 detections of 85 individual adult bull trout in 2004 at the PIT tag weir. Peak movement occurred after dark, 96% of the detections occurring between sunset and sunrise in 2003 and 99% in 2004 (Figure 3). We observed a similar nocturnal movement pattern in 2001 through 2002 in Trestle Creek, but we were unable to validate the time stamp on the PIT tag reader for those years and did not include the data in our analysis.

The total lengths of adult bull trout in Trestle Creek averaged 568 mm (SD = 72.8, range = 335–794, $N = 839$) in 2000, 554 mm (SD = 80.1, range = 380–770, $N = 195$) in 2001, and 549 mm (SD = 74.6, range = 336–770, $N = 383$) in 2002. We recaptured 46 adults in the screw trap that were tagged in 2000, and from 2000 to 2001 their average growth was 28 mm (SD = 14.8, range = 0–86). We recaptured 12 of these individuals again in 2002 and their average growth from 2001 to 2002 was 20 mm (SD = 10.2, range = 5–39).

Age at Emigration for Returning Adults

We collected otoliths from the carcasses of 36 bull trout in 1998 and 11 in 2000. Based on fish size (390–775 mm fork length), we assumed that the dead fish were migratory adults that had returned to Trestle Creek to spawn. We observed rapid growth on the otoliths during the juvenile stage of the fish's life

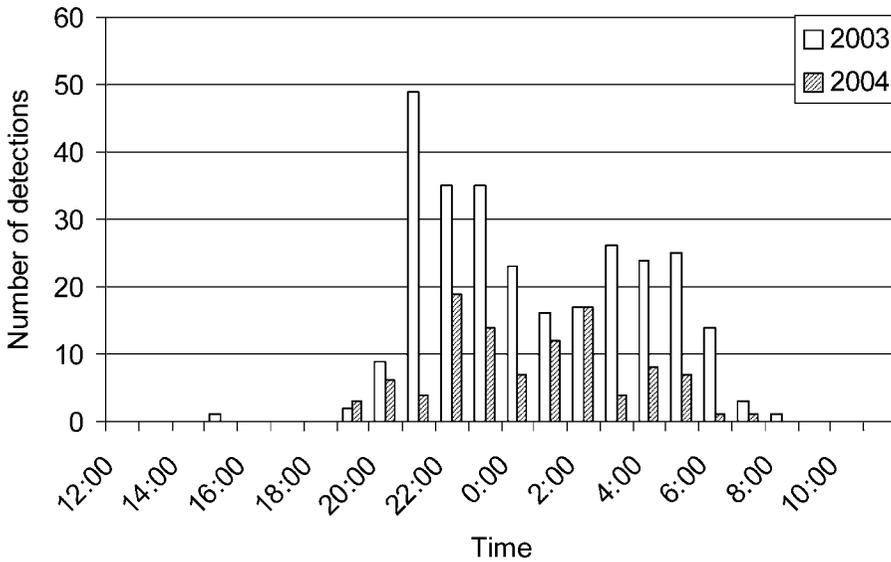


FIGURE 3.—Diel migration patterns of adult bull trout in 2003 ($N = 166$) and 2004 ($N = 85$) in Trestle Creek, a tributary to Lake Pend Oreille, Idaho.

history, and annuli were easily interpreted. As fish matured and entered the lacustrine environment, the width between annuli decreased. We knew that increment width was related to the shift from juvenile to adult habitats, based on changes in Sr/Ca (Figure 2). We estimated that our sampled fish ranged in age from 6 to 11 years (Figure 4a). Although juvenile annuli were easy to count on all otoliths, we found it difficult to interpret the annual growth patterns of older fish, especially the area closer to the edge of the otolith.

Based on otolith microchemistry, these fish emigrated from Trestle Creek for the first time between ages 1 and 5 (Figure 4b). None of the fish in our sample appeared to be age-0 emigrants. About 40% of the fish migrated from the stream to the lake during spring, 13% moved during summer, and 43% moved in fall. We were unable to determine the season when 4% of the fish moved, nor were we able to determine spawning frequency.

Seasonal Timing and Rate of Juvenile Migration

Age-1 and older juvenile bull trout emigrated from Trestle Creek in two pulses in 2001 and 2002. The first pulse occurred in the spring as water temperature and stream discharge increased (Figure 5). Emigration declined in the summer as water temperatures continued to increase and flows dropped. A second pulse occurred during fall as water temperatures declined and fall precipitation began. A similar spring and summer emigration pattern was observed in 2000, but the screw

trap was removed on September 7 and probably missed most of the fall pulse of downstream movement.

We captured 1,611 age-0 bull trout in the screw trap in 2000, 6,563 in 2001, and 4,656 in 2002. Across all years, the catch of age-0 bull trout peaked in the spring, coinciding with high flows and increasing water temperatures (Figure 6). The catch of age-0 bull trout in the screw trap dropped off dramatically as flows decreased, to the point where they were only captured infrequently by late summer and fall.

We rejected the null hypothesis that days with zero age-0 emigrants captured were distributed in proportion to the distribution of temperature and gauge height bins ($\chi^2 = 118.29$, $df = 6$, $P < 0.05$) and likewise for age-1 and older emigrants ($\chi^2 = 132.97$, $df = 6$, $P < 0.05$). Based on ANOVA results, we also rejected the null hypothesis that mean catch per day was the same across the gauge height and water temperature bins ($P < 0.05$). In general, both analyses suggested that fewer age-0 and age-1 and older juveniles moved during low or moderate flows and low temperatures and that more fish moved at higher flows and moderate temperatures.

Juvenile bull trout traveled from the screw trap release area to the mouth of Trestle Creek, where they were detected by the PIT tag station at a mean rate of 455 m/night ($SD = 465$, $N = 40$) in 2001 and 423 m/night ($SD = 407$, $N = 17$) in 2002. Three individuals traveled 1,475 m in 1 night; however, this was the maximum distance over which migration was measured.

The maximum water temperature recorded for

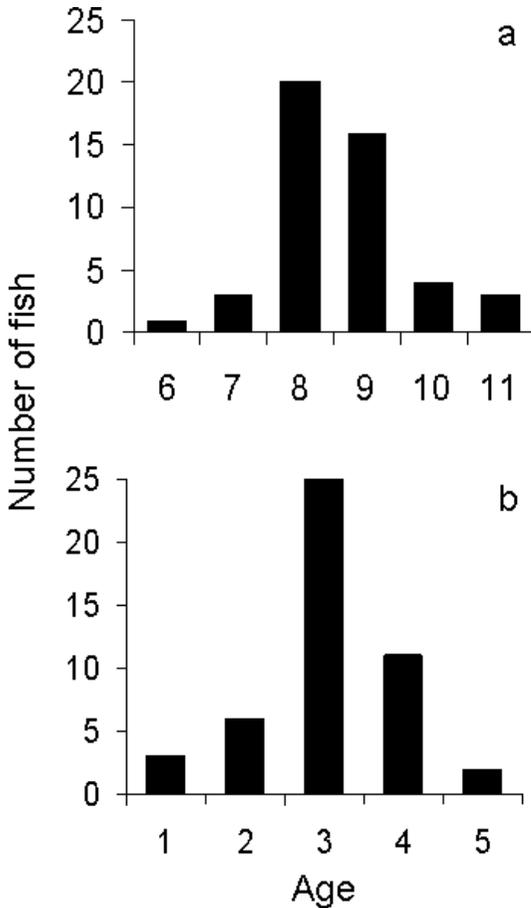


FIGURE 4.—(a) Age of bull trout carcasses that were found in and along Trestle Creek, Idaho, and (b) age at which these fish emigrated as juveniles (i.e., for the first time) from Trestle Creek to Lake Pend Oreille ($N = 47$).

Trestle Creek was similar across the trapping years. Water temperature reached a high of 13.0°C in 2000, 10.9°C in 2001, and 12.7°C in 2002. Flows peaked in the spring, consistent with the snowmelt-dominated hydrology of the area.

Discussion

Adult Spawning Frequency and Growth

Our data suggest that most adfluvial bull trout in Trestle Creek spawn annually and repeat spawners compose a substantial proportion of adult escapement each year. These results are consistent with data collected on the Wigwam River, British Columbia, which drains into Kootenai Reservoir via the Elk River, where annual repeat spawning of adfluvial bull trout outnumbered alternate-year repeat spawners by approximately 2:1 (Baxter and Westover 1999). Elle

(1995) reported similar results, capturing all repeat-spawning fluvial bull trout in Rapid River, a tributary to the Salmon River, in consecutive years. Both annual and alternate-year spawning by bull trout occur in other systems (Fralely and Shepard 1989; Pratt 1992), but studies quantifying the relative proportions are limited.

It is possible that spawning frequency differs for male and female bull trout because of different energy requirements needed for gamete production. However, we were not confident in determining the sex of individual fish, particularly younger males that had yet to develop secondary sex characteristics (e.g., pronounced kipe and spawning coloration). For this reason we did not attempt to analyze repeat spawning by sex. However, due to the high proportion of fish that returned annually, it appears that annual spawning is predominant in Trestle Creek, regardless of sex. Frequency of repeat spawning is an important component when estimating the reproductive potential of individuals within populations, and population modeling efforts that assume annual rather than alternate-year spawning may produce more realistic predictions of long-term persistence of bull trout populations.

The pattern of movement within Trestle Creek suggests that adult bull trout migrate primarily from dusk until dawn within other tributaries to Lake Pend Oreille as well. This may be a mechanism to reduce their vulnerability to predation in smaller stream systems. Using radiotelemetry, Swanberg (1997b) assessed migration patterns of fluvial adult bull trout from the Blackfoot River system in Montana and reported that most adult bull trout moved at night. McPhail and Murray (1979) evaluated the life history of an adfluvial bull trout population in the Upper Arrow Lakes, British Columbia, and based on weir-trapping data, inferred that most upstream movement of adults occurred during the first hours of darkness. Our findings also documented peak movement after dark, so are consistent with previous work. This information may assist managers and regulators to better understand the potential impacts of stream alteration projects on migrating bull trout in areas where bridge, road, or stream restoration construction may impact migratory habitat.

Age at Emigration for Returning Adults

Successful bull trout emigrants ranged from ages 1 to 5, based on our sample of returning adults. For comparison, Ratliff (1992) reported that most juvenile bull trout in the Metolius River–Lake Billy Chinook system emigrated from natal streams at ages 2 and 3. Fralely and Shepard (1989) reported juvenile bull trout emigrants ranging from ages 1 to 4, approximately 80% being ages 2 and 3. Although the range of age at emigration in our study is similar to other studies, we

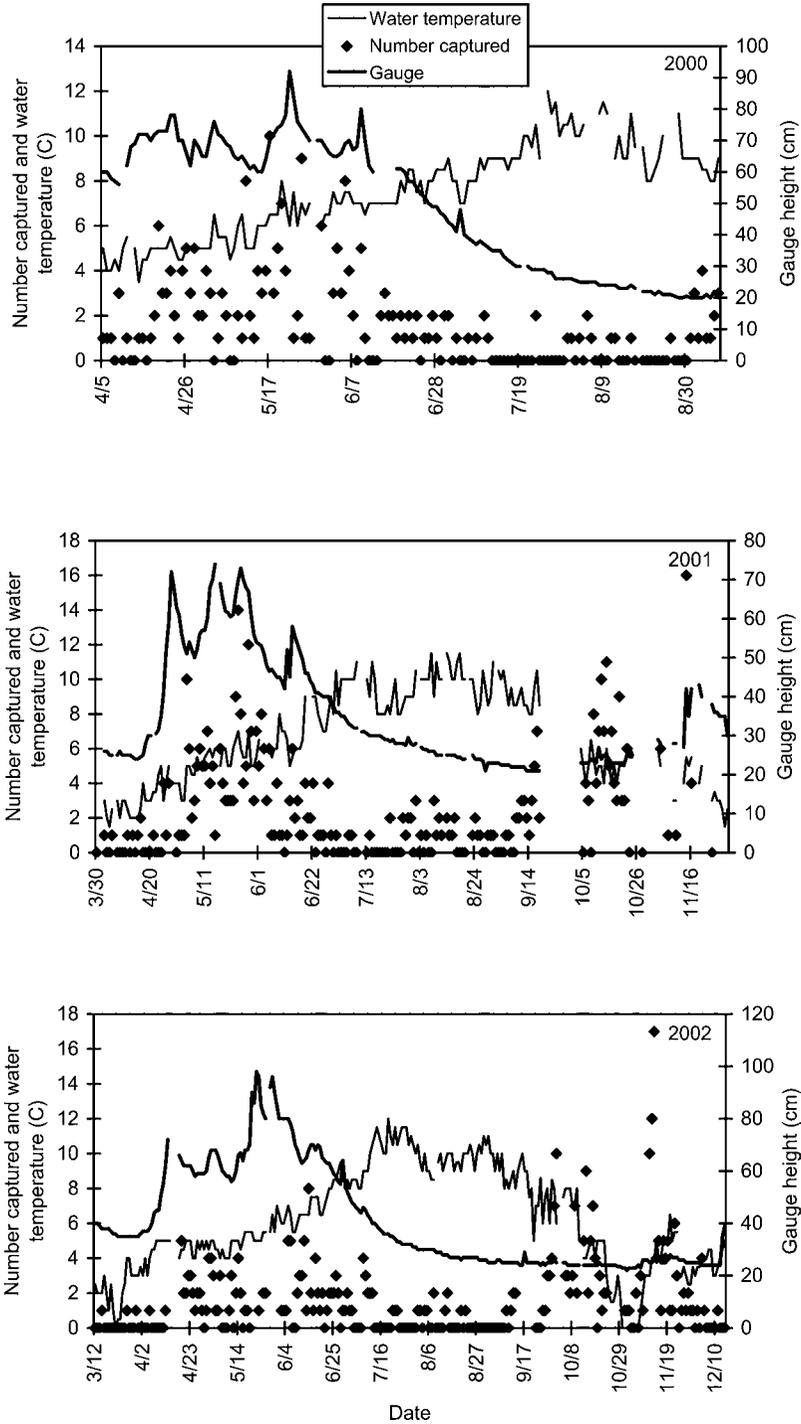


FIGURE 5.—Seasonal migration patterns for age-1 and older juvenile bull trout captured in a screw trap in Trestle Creek, Idaho, in 2000, 2001, and 2002, as related to gauge height and water temperature. Water temperatures represent readings generally recorded midmorning during trap checks.

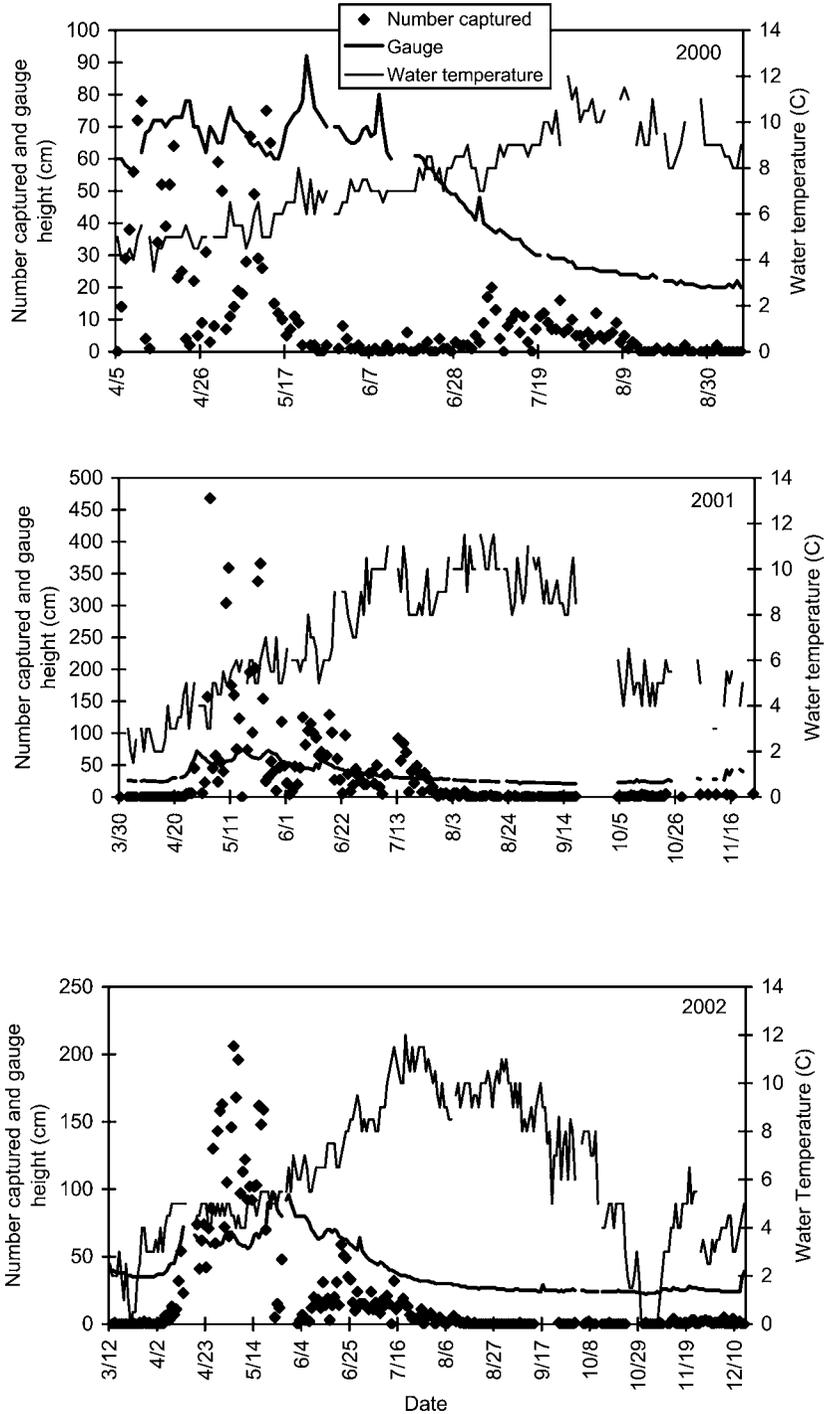


FIGURE 6.—Seasonal migration patterns for age-0 bull trout captured in a screw trap in Trestle Creek, Idaho, in 2000, 2001, and 2002, as related to gauge height and temperature. Water temperatures represent readings generally recorded midmorning during trap checks.

observed a distribution skewed slightly to older emigrants (ages 3 and 4) that came back to spawn. A key difference in our data compared with others is that our age data are based on returning adults rather than emigrating juveniles. This may be the result of enhanced lake survival due to emigration at older ages (and presumably larger size), or Trestle Creek bull trout may emigrate at older ages. Our sample size of otoliths from juvenile emigrants collected in Trestle Creek was limited to incidental mortalities and was not adequate to develop a comprehensive age-frequency distribution to evaluate this question.

Otolith microchemistry has the potential to benefit other researchers investigating inland salmonid recruitment and life history. Based on our otolith analysis, we determined that age-0 bull trout do not appear to survive well in the lake environment because in our sample no age-0 emigrants were detected returning to spawn. Limburg (2001) used a similar retrospective otolith microchemical approach to assess size-biased survivorship, as the result of migration, of American shad *Alosa sapidissima* in New York's Hudson River. The authors noted demographic restructuring of the population due to differential mortality of age-0 shad during emigration, although the pattern of survival appeared to be related to migration timing rather than size alone. Had we relied solely on trap data, we may have concluded that the large number of migrating age-0 bull trout played a key role in maintaining adult escapement.

Our sample of adult otoliths was small compared with the thousands of age-0 fish that move to the lake each year, and a larger sample of adult otoliths, collected over additional years, would improve our understanding of the recruitment of age-0 emigrants to the spawning population. Our trap was located about 1.4 km upstream of the mouth of Trestle Creek, and some age-0 migrants may have found rearing habitat downstream of our trap location, rather than move into the lake. However, it is unlikely that this limited amount of stream was able to provide habitat for the thousands of migrants that were moving past our trap. These results suggest that maintaining high-quality rearing habitat is important to allow juveniles to reach larger sizes before emigrating to the lake environment and to ultimately improve recruitment and adult escapement in adfluvial bull trout populations.

Seasonal Timing and Rate of Juvenile Migration

We observed a large-scale migration of adfluvial bull trout fry soon after their emergence during high spring flows across all years. The downstream movement of these young fish may result from flushing flows or from fish seeking territories. In a long-term

study of migratory brown trout, Elliott (1990) found that the critical period for fish survival is immediately after emergence, when the density-dependent mortality rate is high because fish compete for limited resources that are critical to their survival and growth. Chapman (1962) observed aggressive territorial behavior in the fry of coho salmon *Oncorhynchus kisutch* and concluded it was an important factor in their downstream movement. Fry that move directly to the lake environment may not find the food resources needed to survive or cover resources needed to avoid predation.

Following the large pulse of age-1 and older juveniles emigrating in spring, we observed a second peak in downstream movement in fall, which followed a period of low emigration in late July and August. We saw the same pattern when analyzing otolith microchemistry. McPhail and Murray (1979) hypothesized that two migration peaks may occur, the first in spring (newly-emerged fry) and the second in fall (older juveniles). Similarly, Bellerud et al. (1997) identified two emigration peaks of juvenile bull trout separated by a period of low movement in July in Oregon's Grand Ronde River system. They noted that the peak in spring movement mimicked the peak in high spring flows, whereas the fall emigration appeared to correlate with declining water temperatures. In fall, as water temperatures dropped, we observed an increase in emigration from the low summer movement levels. Fall migration was often associated with rain or rain on snow at low elevations, which generally increased water temperatures and streamflow at each occurrence. These fall movements may be partially related to competition for preferred winter habitats, identified as unembedded cobble substrate in Trestle Creek (Bonneau and Scarnecchia 1998) and other Idaho stream systems (Thurow 1997). Juvenile emigration in Trestle Creek was different than the emigration pattern reported by Fraley and Shepard (1989) for tributaries to the upper Flathead River system. They sampled from June through October with box traps and weirs that could not be fished during high spring flows and, thus, reported emigration of juvenile bull trout from June through August. We were able to observe significant fish movement in spring because we sampled from April to June and used a trapping method that can be implemented during high flows.

Little information is available regarding migration rates for juvenile bull trout (Pratt 1992). Fraley and Shepard (1989) speculated that juvenile bull trout move downstream rapidly, which is similar to our study. Our migration rate data are limited in scale because we were studying a single tributary to Lake Pend Oreille, and we were limited to studying individual fish moving primarily in fall under low flow conditions. It appeared

that some of the individuals were not actively migrating when initially captured, as evidenced by travel times exceeding 90 d for 7 of the 57 individuals in our study. These individuals would have skewed (reduced) our estimates of emigration rates. Had we excluded these individuals from the analysis, the migration rates would have been 79 m greater per night in 2001 and 26 m greater per night in 2002. The maximum distance traveled that we observed in 1 night was 1,475 m by three individuals; however, this was the maximum distance over which migration was measured. Juvenile bull trout have the potential to migrate at higher rates in small systems such as Trestle Creek. For example, migration rates for individuals moving in the spring may be faster because of higher stream flows. Nonetheless, the rates we report are the only published data we are aware of for juvenile bull trout emigration.

Conclusion

Diverse life history patterns, such as spawning frequency and migration timing, are important to the persistence and stability of bull trout populations (Rieman and McIntyre 1993). In our study we describe the diversity in spawning frequency and migration of a relatively strong adfluvial population of bull trout, thereby contributing to the understanding of different life history strategies exhibited by bull trout. Through the use of otolith microchemistry we discovered that many of the age-0 emigrants may not be surviving to adulthood, demonstrating that assumptions we make based on traditional sampling methods might not provide the complete picture. Ensuring the availability of high-quality habitat in tributaries that meets the needs of older (larger) juveniles is important in maintaining recruitment and adult escapement. These results help to increase the understanding of bull trout population dynamics, critical to developing comprehensive restoration and management strategies for bull trout.

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References

- Baxter, J. S., and W. T. Westover. 1999. Wigwam River bull trout: habitat conservation trust fund progress report (1998). British Columbia Ministry of Environment, Fisheries Progress Report K054, Cranbrook.
- Bellerud, B. L., S. Gunkel, A. R. Hemmingsen, D. V. Buchannan, and P. J. Howell. 1997. Bull trout life history, genetics, habitat needs, and limiting factors in central and northeast Oregon: 1996 annual report. Bonneville Power Administration, Portland, Oregon.
- Bonneau, J. L., and D. L. Scarnecchia. 1998. Seasonal and diel changes in habitat use by juvenile bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) in a mountain stream. *Canadian Journal of Zoology* 76:783–790.
- Brenkman, S. J., G. L. Larson, and B. E. Gresswell. 2001. Spawning migration of lacustrine-adfluvial bull trout in a natural area. *Transactions of the American Fisheries Society* 130:981–987.
- Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause for emigration. *Journal of the Fisheries Research Board of Canada* 19:1047–1080.
- Downs, C. C., R. Jakubowski, and S. Moran. 2003. Lake Pend Oreille—Clark Fork River fishery research and monitoring: 2002 annual progress report—bull trout redd counts and escapement estimates, 1999–2001. Report to the Avista Corporation by the Idaho Department of Fish and Game, Boise.
- Downs, C. C., and R. Jakubowski. 2005. Lake Pend Oreille—Clark Fork River fishery research and monitoring: 2003 annual progress report—bull trout redd counts. Report to the Avista Corporation by the Idaho Department of Fish and Game, Boise.
- Dunham, J., B. Rieman, and K. Davis. 2001. Sources and magnitude of sampling error in redd counts for bull trout. *North American Journal of Fisheries Management* 21:343–352.
- Elle, S. 1995. Bull trout investigations: Rapid River bull trout movement and mortality studies. Idaho Department of fish and Game, Report F-73-R-17, Boise.
- Elliott, J. M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*, III. The role of territorial behaviour. *Journal of Animal Ecology* 59:803–818.
- Epifanio, J., G. Haas, K. Pratt, B. Rieman, P. Spruell, C. Stockwell, F. Utter, and W. Young. 2003. Integrating conservation genetic considerations into conservation planning: a case study of bull trout in the Lake Pend Oreille—lower Clark Fork River system. *Fisheries* 28(8):10–24.
- Fraleigh, J. J., and B. B. Shepard. 1989. Life history, ecology, and population status of migratory bull trout *Salvelinus confluentus* in the Flathead Lake and river system, Montana. *Northwest Science* 63:133–143.
- Kennedy, B. P., J. D. Blum, C. L. Folt, and K. H. Nislow. 2000. Using natural strontium isotopic signatures as fish

- markers: methodology and application. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2280–2292.
- Kennen, J. G., S. J. Wisniewski, and N. H. Ringler. 1994. Application and modification of an auger trap to quantify emigrating fishes in Lake Ontario tributaries. *North American Journal of Fisheries Management* 14:828–836.
- Limburg, K. E. 2001. Through the gauntlet again: demographic restructuring of American shad by migration. *Ecology* 82:1584–1596.
- McPhail, J. D., and C. B. Murray. 1979. The early life history and ecology of Dolly Varden (*Salvelinus malma*) in the upper Arrow Lakes. University of British Columbia, Vancouver.
- Muhlfeld, C. C., S. Glutting, R. Hunt, D. Daniels, and B. Marotz. 2003. Winter diel habitat use and movement of subadult bull trout in the upper Flathead River, Montana. *North American Journal of Fisheries Management* 23:163–171.
- Nakano, S., K. D. Fausch, T. Furukawa-Tanaka, K. Maekawa, and H. Kawanabe. 1992. Resource utilization by bull charr and cutthroat trout in a mountain stream in Montana, U.S.A. *Japanese Journal of Ichthyology* 39:211–217.
- Nelson, M. L., T. E. McMahon, and R. F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. *Environmental Biology of Fishes* 64:321–332.
- Pratt, K. L. 1992. A review of bull trout life history. Pages 5–9 in P. J. Howell and D. V. Buchanan editors. *Proceedings of the Gearhart Mountain Bull Trout Workshop*. American Fisheries Society, Oregon Chapter, Corvallis.
- Radtke, R. L. 1995. Otolith microchemistry of charr: use in life history studies. *Nordic Journal of Freshwater Research* 71:392–395.
- Ratliff, D. E. 1992. Bull trout investigations in the Metolius River–Lake Billy Chinook system. Pages 37–44 in P. J. Howell and D. V. Buchanan editors. *Proceedings of the Gearhart Mountain Bull Trout Workshop*. American Fisheries Society, Oregon Chapter, Corvallis.
- Rieman, B. E., and C. M. Falter. 1976. Lake Pend Oreille limnological studies. Idaho Department of Fish and Game, Job Completion Report, Project F-73-R-1, Sub-project III, Study I, Job I. Boise.
- Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. U.S. Forest Service, Intermountain Research Station, General Technical Report INT-302, Ogden, Utah.
- Rieman, B. E., and J. D. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. *Transactions of the American Fisheries Society* 124:285–296.
- Rieman, B. E., and D. L. Myers. 1997. Use of redd counts to detect trends in bull trout *Salvelinus confluentus* populations. *Conservation Biology* 11:1015–1018.
- Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of bull trout within the Columbia and Klamath river basins. *North American Journal of Fisheries Management* 17:1111–1125.
- Rieman, B. E., and F. W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. *North American Journal of Fisheries Management* 21:756–764.
- Saffel, P. D., and D. L. Scarnecchia. 1995. Habitat use by juvenile bull trout in belt-series geology watersheds of northern Idaho. *Northwest Science* 69:304–317.
- Schmetterling, D. A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown Dam, Montana. *North American Journal of Fisheries Management* 23:721–731.
- Swanberg, T. 1997a. Movements of bull trout (*Salvelinus confluentus*) in the Clark Fork River system after transport upstream of Milltown Dam. *Northwest Science* 71:313–317.
- Swanberg, T. 1997b. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. *Transactions of the American Fisheries Society* 126:735–746.
- Thurow, R. F. 1997. Habitat utilization and diel behavior of juvenile bull trout (*Salvelinus confluentus*) at the onset of winter. *Ecology of Freshwater Fish* 6:1–7.
- Wells, B. K., B. E. Rieman, J. L. Clayton, D. L. Horan, and C. M. Jones. 2003. Relationships between water, otolith, and scale chemistries of westslope cutthroat trout from the Coeur d'Alene River, Idaho: the potential application of hard-part chemistry to describe movements in freshwater. *Transactions of the American Fisheries Society* 132:409–424.
- Wissmar, R. C., and S. D. Craig. 2004. Factors affecting habitat selection by a small spawning charr population, bull trout, *Salvelinus confluentus*: implications for recovery of an endangered species. *Fisheries Management and Ecology* 11:23–31.
- Zimmerman, C. E., and G. H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. *Canadian Journal of Fisheries and Aquatic Sciences* 57:2152–2162.